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ABSTRACT

Studying phenotypic variations along gradients may provide insights into mechanisms that drive species distributions, and thus can be useful indicators of environmental change. In mountains, the study of phenotypic variation along elevation gradients is of increasing relevance due to impacts of climate change. We analysed European ringing data to unravel the direction of phenotypic variation along elevation gradients in six common and resident songbird species occurring along a wide elevational range. We modelled intra-specific change in wing length, body mass and their ratio with elevation and found a significant increase in wing length and a decrease in body mass at high elevations. The results of our exploratory analysis show the potential that continent-wide ringing databases offer to describe patterns of phenotypic variation along environmental gradients.

Keywords: Alps, Bergmann's Rule, body mass, wing length.

Running head: Phenotypic variation in Alpine birds

INTRODUCTION

Species with high variability in traits may more readily adapt to environmental changes (Lehikoinen *et al.* 2018). Phenotypic variation within species is shaped by the spatial and temporal differences of the habitats in which different populations live and includes differences in morphological traits such as wing length (Poblete *et al.* 2018). Studies of phenotypic variation in relation to the environment are important, as they may reveal fundamental drivers of variation within and between species. For example, Bergmann's Rule proposes that species of larger size tend to be found in colder climates (Bergmann 1847), a concept that has also been extended to variation within species, although support is not universal (Blackburn *et al*. 1999). Furthermore, studies of phenotypic variation may reveal sensitivity to environmental change. For example, recent studies have documented evidence that morphological changes in mountain birds (Delgado *et al.* 2019) and migratory passerines (Weeks *et al.* 2019) are correlated with climate change.

Along elevation gradients, numerous factors shape phenotypic adaptations. Variables that are causally related to elevation include ultraviolet radiation, oxygen levels, and (of particular relevance to phenotypic adaptation) temperature and air pressure. Bergmann's Rule is used to explain morphological differences across climate gradients, predominantly from warmer to colder environments (Meiri & Dayan 2003). There is some evidence for larger individuals (i.e. a higher body mass) with relatively shorter extremities, e.g. legs and wings, at high elevations (Laiolo & Rolando 2008, Meiri & Dayan 2003, Poblete *et al.* 2018). This may arise through selection for larger animals that have a lower surface area to volume ratio than smaller animals, so they radiate less body heat per unit of mass, in agreement with Bergmann's Rule. Conversely, a preponderance of smaller individuals (a combination of different length measurements and body mass) has been reported at higher elevations (Lundblad & Conway 2019), as have smaller individuals (body mass) with longer wings (Bears *et al*. 2008, Lu *et al.* 2009). The latter seems reasonable as smaller bodies require lower energy intake, which might be a limiting factor in high elevation habitats with seasonally variable resource availability. For example, Freeman (2017) found little evidence for body size clines within tropical bird species, but where there were differences, they were inconsistent with Bergmann's Rule. Similarly, Boyce *et al.* (2019) found that body mass of Bornean mountain birds decreased with elevation whereas relative tarsus length increased. The authors argued that phenotypic adaptation is more likely to be driven by the foraging mode of high elevation species, rather than temperature (Boyce *et al.* 2019). In both of these studies, wing length was not related to elevation,

even though other studies have argued that longer wings reduce the cost of flying at lower air pressure (Scott 2011) and may increase aerodynamic performance (Altshuler & Dudley 2006). Furthermore, flying in oxygen-thin environments requires physiological and morphological adaptations to enable the birds to cope with hypoxia and to reduce the metabolic cost of staying aloft (Barve *et al.* 2016, Scott 2011). A concensus on the association between phenotypic adaptations and elevation is therefore lacking, possibly because there have been few large-scale investigations on this topic.

We aimed to assess whether there was a trend in intra-specific morphological variation in songbird species along elevation gradients. We analysed the variation in two phenotypic traits (wing length, body mass) and their ratio (i.e. wing length relative to body mass) within six different songbird species that occur along elevation gradients in the breeding and post-fledging period (spring and summer). We used ringing data retrieved from the EURING Data Bank (du Feu 2019), the coordinating organisation for European bird ringing schemes, and collected mainly in the Alps and their foothills.

METHODS

We selected species breeding along a continuous elevation gradient from 0 to >2000 m.a.s.l. based on information in BirdLife International (2019), and from digital elevation maps available in www.ornitho.it. Furthermore, we selected species which are classified as residents and/or facultative short-distance migrants (del Hoyo & Christie 2006, Glutz von Blotzheim & Bauer 1991), as long-distance migration itself shapes wing morphology (Fiedler 2005). We requested all available ringing data of birds captured and recaptured frequently (Fasano *et al.* 2018) in our prior defined Alpine landscape (44°N - 48°N, 4°E - 16°E, Switzerland, France, Italy, Austria, Germany, Slovenia) from the EURING database. These data included captures from outside the defined area (e.g. northern France, northern Germany, Sweden) if birds were then recovered inside this area (Fig. 1). Within the data set of all 14 species, we selected only adults that were first captures (to exclude pseudoreplication). Although we restricted our species to those that are mainly resident in the study region, we cannot exclude altitudinal migration during winter (Barcante *et al.* 2017, Boyle 2017, Hsiung *et al*. 2018). Furthermore, some of our species are known to disperse over short distances within their ranges, including some longer distance movements within Europe, e.g. Black Redstart *Phoenicurus ochruros*, Eurasian Blackbird *Turdus merula* (del Hoyo & Christie 2006, Glutz von Blotzheim & Bauer 1991). We therefore excluded captures outside the period May to September to minimise the chances of including migrant individuals breeding at

other elevations than those expected from the ringing location (for brevity henceforth referred to as 'breeding birds'). After filtering the records following the above criteria, we selected those species for which we had sufficient records across the elevation gradient (10 % of all records per species had to be from locations above 1200 m.a.s.l.) and which had biometric data, i.e. wing length (as measured by the length of 3rd primary) and body mass. They were Eurasian Blackbird, Eurasian Wren *Troglodytes troglodytes*, Coal Tit *Periparus ater*, Goldcrest *Regulus regulus*, Black Redstart and Willow Tit *Poecile montanus*.

Statistical Analyses

As wing length is allometrically correlated with body mass (i.e. that individuals with longer wings also have higher body masses, Fig. S1) and both may be a proxy for body size, we calculated the ratio of wing length to the cubic root of body mass ($wing\ length/\sqrt[3]{body\ mass}$, henceforth wing:mass ratio) to analyse the differences in relative wing length between individuals breeding at low and high elevations. To allow direct comparison of effect sizes across species, we scaled all biometrics at the species level (z-score). To assess how wing length, body mass and wing:mass ratio varied as a function of elevation, we used linear mixed effect models, using the 'lmer' function in R 3.4.2 (R Core Team 2019), assuming normally distributed errors. The models included elevation as an explanatory variable, which we considered in two different ways in separate models: first, as a continuous variable, and second as a categorical variable. Following the definition of mountain habitat for the Alps (Lehikoinen *et al.* 2018), we defined locations <1200 m.a.s.l. as low and >1200 m.a.s.l. as high elevations. Grouping the birds according to high and low elevations reflects the ecological context of this study, whereas showing the effect along a continuous gradient gives information about the distribution of our data.

Wing length, body mass and wing:mass ratio (all scaled) were analysed as response variables in three separate models in relation to elevation. We were interested in general trends with elevation across Alpine birds, hence we pooled all species for the analysis and set species as a random effect in all six models (i.e. three different response variables in relation to two different measures of elevation) to account for the fact that variation in scaled traits may be species-specific. However, we also ran the same models for each individual species (without the random term) to determine the extent to which individual species associations were consistent with the overall trends. There is evidence that biometrics of birds have changed over time in relation to increasing global temperatures due to climate change (Delgado *et al.* 2019, Weeks *et al.* 2019). To account for

possible temporal trends over our time period of 36 years, we tested the effect year by including it as a fixed effect in the overall model and comparing AIC values for models with and without year. Additionally, we performed linear models for each species including year.

Analysis of model residuals did not show any violation of the model assumptions. We used Bayesian methods to obtain uncertainty estimates of the model parameters (Korner-Nievergelt *et al.* 2015) and therefore to account for the uncertainty of the model estimates and model predictions. Following Korner-Nievergelt *et al.* (2015), we used improper prior distributions, namely $p(\beta) \sim 1$, for the coefficients and $p(\sigma) \sim 1/\sigma$ for the variance parameters and furthermore obtained posterior distributions of the respective models by simulating 5000 values from the joint posterior distributions of each model's parameter, applying the function 'sim' included in the package 'arm' (Gelman & Hill 2007). For the respective model estimates, we used the means of the simulated values from the joint posterior distributions of each model's parameter and the 2.5% and 97.5% quantiles as limits for the 95% credible intervals (CrI; Korner-Nievergelt *et al.* 2015). The effect of a variable was declared as significant if the corresponding 95% CrI did not include zero or if the 95% CrIs of the comparative groups (low and high elevation) did not overlap.

RESULTS

After selecting six target species with sufficient sample sizes, the raw data from EURING contained 79,653 records, of which 30,426 were first captures and 12,805 fitted our time period of May to September. Of these, only 1,445 records contained biometrics (11% of all first captures during the breeding season; see Table S1 for sample sizes according to species), and, despite having considered data from a total of six countries, only data from the Swiss Ringing Scheme were usable. The records spanned a 36 year period (1982 – 2018, mean: 2010, 1st quartile: 2008, 3rd quartile: 2015), and presented an overall elevation gradient from 95 m.a.s.l. to 1,900 m.a.s.l (mean: 962 m.a.s.l., 1st quartile: 462 m.a.s.l., 3rd quartile: 1,233 m.a.s.l.). The locations of first captures were widely distributed across Europe, but the majority of the records was located within or close to the Alps (Fig. 1; see Fig. S2 for heatmaps).

When considering the two elevation categories, there were n= 908 records for the low elevation group and n = 534 records for the high elevation group. In the overall model, the year had no significant effect on the

biometrics and did not improve the model in terms of AIC, hence it was not considered further (Table S2). We additionally tested the effect of year on the wing:mass ratio in single-species models and found a positive effect in Coal Tit, indicating their wings increased in length relative to body mass over a period of 30 years (Fig. S3), but not in any other species, nor in the combined-species model.

We found a significant positive effect of elevation (continuous) on scaled wing length, which increased by 0.15 mm (95% CrI: 0.04 − 0.27) per 1000m increase in elevation. Body mass was found to decrease significantly with elevation (β = -0.11, 95% CrI: -0.21 − -0.01). The wing:mass ratio also increased significantly with elevation (β = 0.14, 95% CrI: 0.09 – 0.20). When records were grouped into high and low elevation, the results were similar, with a positive effect on wing length (β = 0.15, 95% CrI: 95% CrI: 0.02 − 0.28) and wing:mass ratio (β = 0.20, 95% CrI: 0.12 – 0.28; Table 1, Fig. 2). In all models, a lot of variation was unexplained, resulting in very low R^2-values (<0.1, Table 1). For single-species models, parameter estimates were in general in accord with those of the combined-species model in terms of direction of effect. There was stronger support (i.e. a significant effect) for longer wings in Blackbird and Willow Tit), lower body masses in Coal Tit and increasing wing:mass ratio in Blackbird and Coal Tit, with increasing elevation. However, Willow Tit body mass showed the opposite trend to the overall model, significantly increasing with elevation (Table S3).

DISCUSSION

Individuals breeding at high elevations were generally smaller and had longer wings. Wing:mass ratio increased with higher elevations, i.e. wing length increased relative to body size along the gradient, which was driven by both increases in wing length and decreases in body mass (Table 1, Fig. 2). These associations were, however, fairly weak in terms of the variation explained by the models, and for body mass, in terms of the consistency of results at the species level.

Interestingly, our results do not provide much support for Bergmann's rule, which predicts shorter wings and larger bodies in colder (therefore higher elevation) environments (as shown by Laiolo & Rolando 2008, Meiri & Dayan 2003, Poblete *et al.* 2018). The combined-species model suggested a general decrease in body mass with elevation, although at the individual species level (Table S3), there was a single species, Willow Tit, that showed an increase in body mass. There was more consistency in associations between wing length and elevation,

longer wings being evident in combined-species models and in most individual species (although only two were significant). Similar results have been found in individual species. For example, female Dark-eyed Juncos *Junco hyemalis* breeding at high elevations had longer wings and shorter tarsi (a measure of body size; Bears *et al*. 2008), and snowfinch *Montifringilla* species were smaller (in terms of body length, bill length, body mass, tarsus length) with longer wings and a higher ratio of wing length and body size at high elevation sites (Lu *et al*. 2009).

Along an elevation gradient, temperature (the variable hypothesized to explain Bergmann's Rule) might not be the only determining factor shaping bird morphology. Indeed, in tropical mountain systems, it has been shown to be of lower importance for trait variations along elevation gradients (Boyce *et al.* 2019, Freeman 2017); instead, flying in thin air (lower air pressure at high elevations) and the necessity to increase flight performance (due to stronger winds) might select for longer wings (Altshuler & Dudley 2006, Bears *et al.* 2008). The seasonality of resource availability in higher elevation habitats, e.g. the later peak in insect abundance due to snow cover (Bears et al. 2003), hypoxia and climate severity (Bears et al. 2008) may further lead to an advantage of having a small body in order to reduce the amount of energy needed. It is possible that these factors selected for smaller body sizes in high elevation habitats, but there may also be direct effects that restrict the growth of morphological traits, such as body mass, during the individual's lifetime.

Although our results give some support to phenotypic adaptation to lower air pressure at higher elevations, it must be acknowledged that there are many potentially important drivers that vary along the gradient which were unable to take into account. For example, it is known that variation in wing morphology within species may be influenced by the degree of forest fragmentation (e.g. Fiedler 2005, Desrochers 2010) which could vary from more anthropogenically disturbed lowlands to mountain forests. Additionally, wing morphology may vary according to foraging habitat, as round-winged species have been shown to forage closer to the ground, whereas species with more pointed wings forage more commonly in trees (Marchetti *et al.* 1995). Furthermore, the influence of environmental factors such as forest cover and fragmentation may vary at large geographical scales. Our sample was derived from a relatively large area in order to maximize sample size. The availability of a larger sample of biometrics from ringed birds (see below) would also allow habitat and geographical influences (e.g. latitude) to be estimated.

Unfortunately, the data were not sufficient to account for sex and age. In addition to effects of environmental variables (see above), we assume that a large proportion of the unexplained variation in our models comes from morphological differences between males and females, as shown for songbirds in similar studies (Bears *et al.* 2008, Lu *et al.* 2009). Furthermore, our measure of body size (body mass) is likely to vary between individuals and may be sensitive to fine-scale seasonal and even diel variations that we were not able to take into account. Nevertheless, we would expect that body mass represents a reasonable, although fairly approximate, measure of body size. A better measure of body size would be one related to skeletal growth, such as relative tarsus length, which is likely to be less temporally variable (Bears *et al.* 2008), but which was not available on the EURING Data Bank. Another reason for the relatively weak effect of elevation on the morphological traits is that we used species occurring across the entire elevation gradient instead of comparing subspecies of low and high elevation. Additionally, due to the habitat requirements of the species we have chosen (mostly forest species), we do not have data from very high elevation habitats above the tree-line, where environmental cues may exert stronger pressures on the breeding and survival of birds (Lu 2005), in particular to cope with hypoxia (Barve *et al.* 2016), although within the studied region, possibly only Black Redstart would occur at these elevations in addition to lower elevation habitats.

This study has used a continental-scale database to analyse phenotypic variability in passerine species across elevation gradients. Whilst we find some intriguing results, in particular individuals at higher elevations having lower body mass and relatively longer wings, we were restricted in the conclusions that we were able to draw due to the availability of the data. To better understand phenotypic adaptations of birds to elevation, we highlight the importance of the collection of biometric ringing data, especially for high elevation populations, where data from breeding periods is lacking for many species. We suggest that ringers always record wing length (both, 3rd primary and maximum wing length) and tarsus length, as well as body mass. Furthermore, the scientific potential of standardised bird ringing could be higher if we were able to improve the data transfer from national ringing schemes to the EURING Data Bank. Even though measurements are commonly taken within the standard protocols in all European ringing schemes, we only located usable data from the Swiss Ringing Scheme. Enhancing biometric data availability at the European scale would greatly enhance our ability to study species adaptations.

The current literature covers almost exclusively tropical mountain ecosystems, and comparative within-species studies in temperate regions are lacking, which might be an additional reason for the inconsistency in the results. European-wide or even global ringing datasets have a huge potential to address questions regarding the phenotypic adaptations to different environments within the same species and their response to climate change (as there are indications for changes in morphology within the last decades, e.g. Fig. S3, and Delgado *et al.* 2019, Weeks *et al.* 2019). Further studies with larger biometric datasets (especially for high elevation populations of species) may even enable us to analyse differences in morphological variability between specialists and generalists, species of different habitat types (open grassland vs. forest), or differences in the degree of phenotypic plasticity between single species or subspecies (see Fig. S4 for visual comparison of the variability in traits between the study species, showing slightly higher variability in the data of Blackbirds and Coal Tits). Ultimately, we might be able to use phenotypic traits as predictors for the ability of a species to shift their range, and to assess whether they are more resilient and/or resistant to environmental changes.

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Table 1. Effect of elevation (continuous in m x 10^3, and categorical) on the bird's scaled (z score) wing length, body mass and wing:mass ratio, modelled with linear mixed effect models (LMMs). The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects of elevation are given in bold. *N* = 1442 in each case.

LMM	Intercept	Estimate (elevation)	Marginal R^2	Conditional R^2
Wing length ~ elevation (continuous) + (1|Species)	-0.157 (95% CrI: -0.292 − -0.022)	**0.153** **(95% CrI: 0.040 - 0.270)**	0.007	0.010
Body mass ~ elevation (continuous) + (1|Species)	0.119 (95% CrI: 0.002 − 0.238)	**-0.111** **(95% CrI: -0.210 - -0.010)**	0.004	0.005
Ratio ~ elevation (continuous) + (1|Species)	-0.23 (95% CrI: -1.44 – 1.01)	**0.140** **(95% CrI: 0.09 – 0.20)**	0.002	0.930
Wing length ~ elevation (categorical) + (1|Species)	-0.061 (95% CrI: -0.153 − 0.031)	**0.145** **(95% CrI: 95% CrI: 0.017 – 0.279)**	0.005	0.008
Body mass ~ elevation (categorical) + (1|Species)	0.058 (95% CrI: -0.020 − 0.140)	-0.120 (95% CrI: -0.241 − 0.004)	0.004	0.005
Ratio ~ elevation (categorical) + (1|Species)	-0.160 (95% CrI: -1.38 – 1.060)	**0.198** **(95% CrI: 0.120 – 0.277)**	0.004	0.930

Figure 1. Locations of all first captures during breeding season (May – September) for each species. Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the whole dataset are given in Table S1.

Figure 2. Intra-specific morphological variation of passerines along an elevation gradient. Plots show combined data of six species. Scaled measures wing length, body mass and wing:mass ratio along a continuous elevation gradient were analysed. Regressions are black solid lines and the corresponding 95% CrI are in grey, when the effect was significant. Right below: Differences in scaled measures wing length (filled circle), body mass (circle) and wing:mass ratio (square) between captures from low (<1,200 m.a.s.l.) and high (>1,200 m.a.s.l.) breeding grounds. Results of the appropriate LMMs are provided in Table 1.

SUPPLEMENTARY ONLINE MATERIAL

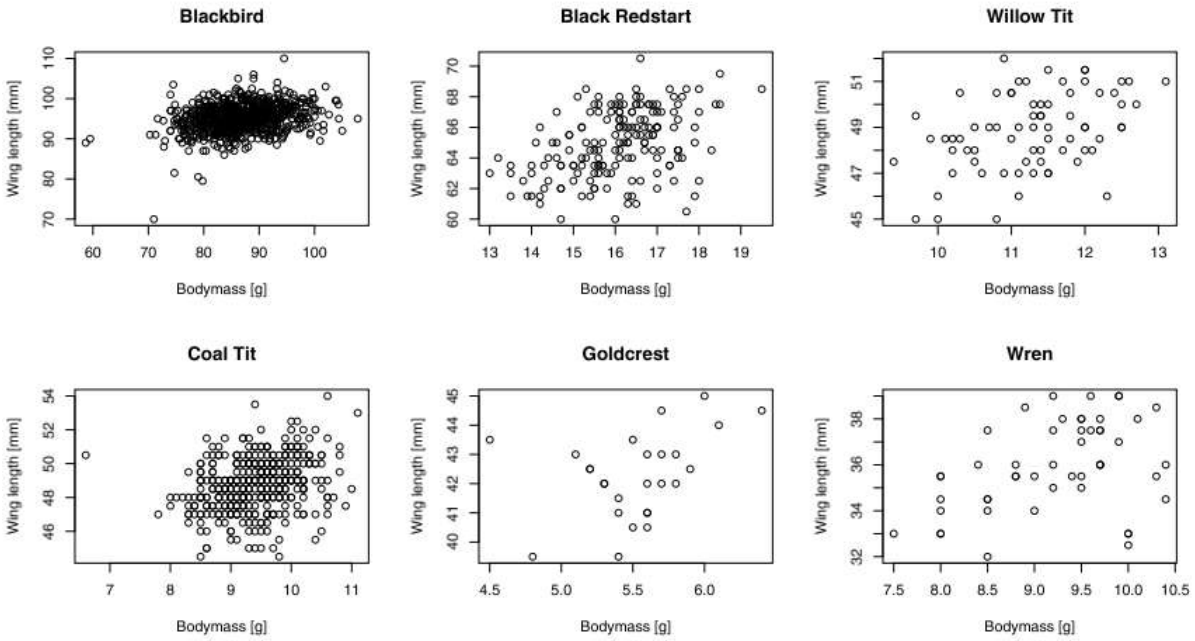

Figure S1. Associations between wing length and body mass for all six study species. The unscaled raw data are shown. Sample sizes for each species are given in Table S1.

Table S1. Sample sizes of each species included in the analysis (Number of records with biometrics). Number of records from birds captured above 1,200 m.a.s.l. are given in brackets. Ringing records were included if, for each individual (first capture during breeding season), location, date, wing length and body mass was available (% of records with biometrics).

Species	**Total no. of records in Data bank**	**No. of adult first captures**	**No. of first captures during breeding season**	**No. of records with biometrics**	**% of records with biometrics**
All species	79,653	30,426	12,805	1,442 (908)	11
Blackbird *Turdus merula*	53,811	20,039	8,844	739 (61)	8
Eurasian Wren *Troglodytes troglodytes*	8,285	3,195	485	50 (13)	10
Coal Tit *Periparus ater*	7,633	3,210	1,936	388 (364)	20
Goldcrest *Regulus regulus*	5,437	2,272	441	26 (21)	6
Black Redstart *Phoenicurus ochruros*	3,026	1,168	706	170 (15)	24
Willow Tit *Poecile montanus*	1,461	542	393	72 (62)	18

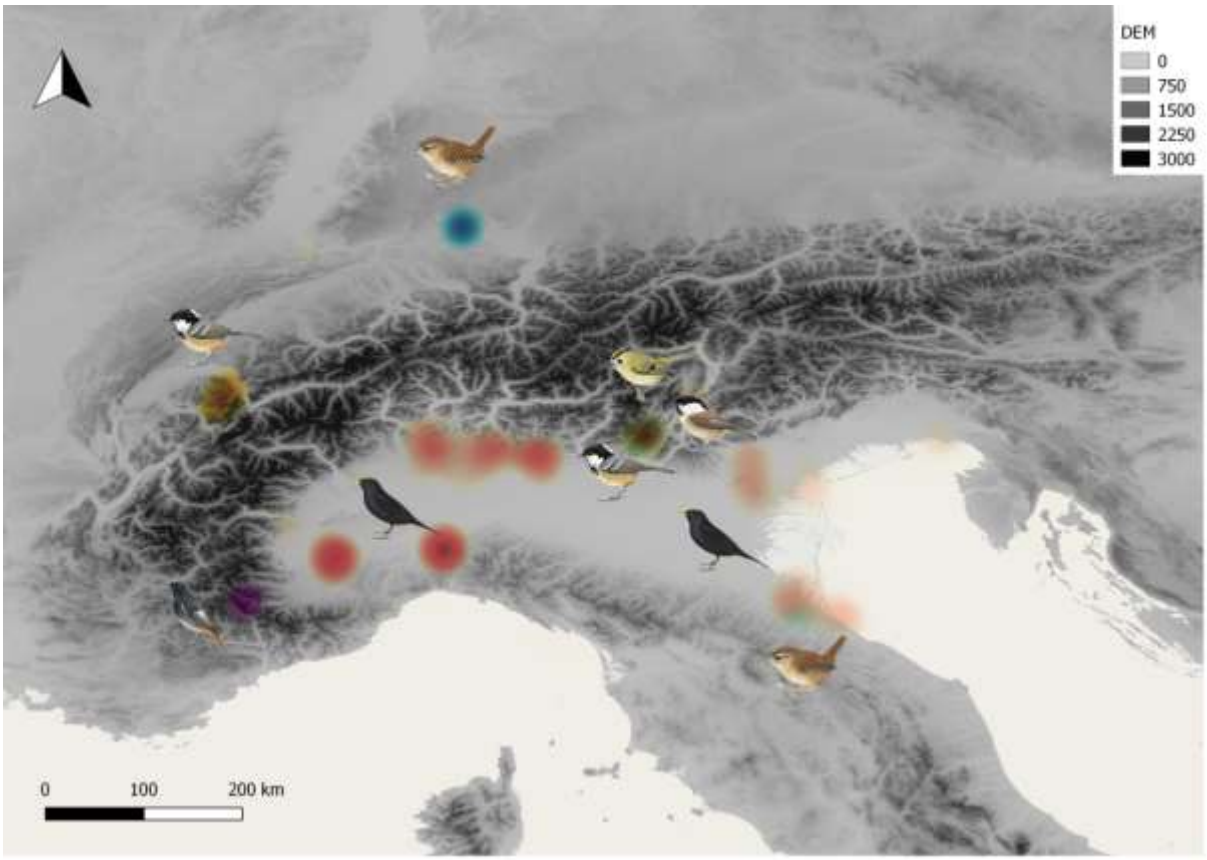

Figure S2. Species-specific heatmaps for locations of first captures (Blackbird: red, Eurasian Wren: blue, Coal Tit: orange, Goldcrest: green, Black Redstart: purple, Willow Tit: yellow). Origin of ringing data retrieved from EURING, entirely collected by the Swiss Ringing Scheme. Sample sizes of the dataset used in the analysis are given in Table S1 and their distribution across the whole area in Figure 2 (main text).

Table S2. Effect of elevation (continuous (in m x 10^3)) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio between both, modelled with linear mixed effect models (LMMs, function 'lmer'), including year as fixed effect. The effect is significant if the 95% Credible interval (CrI) does not include zero. Significant effects are given in bold. ΔAIC is the difference between the model without year (that used in the main text) and the model including year as a fixed effect (that presented here). *N* = 1442.

LMM	Intercept	Estimate (elevation)	Estimate (year)	Marginal R^2	Conditional R^2	ΔAIC
Ratio ~ elevation + year + (1|Species)	-4.86 (95% CrI: -12.19 – 2.54)	**0.136 (95% CrI: 0.080 – 0.190**	0.002 (95% CrI: -0.001 – 0.006)	0.002	0.930	0.5

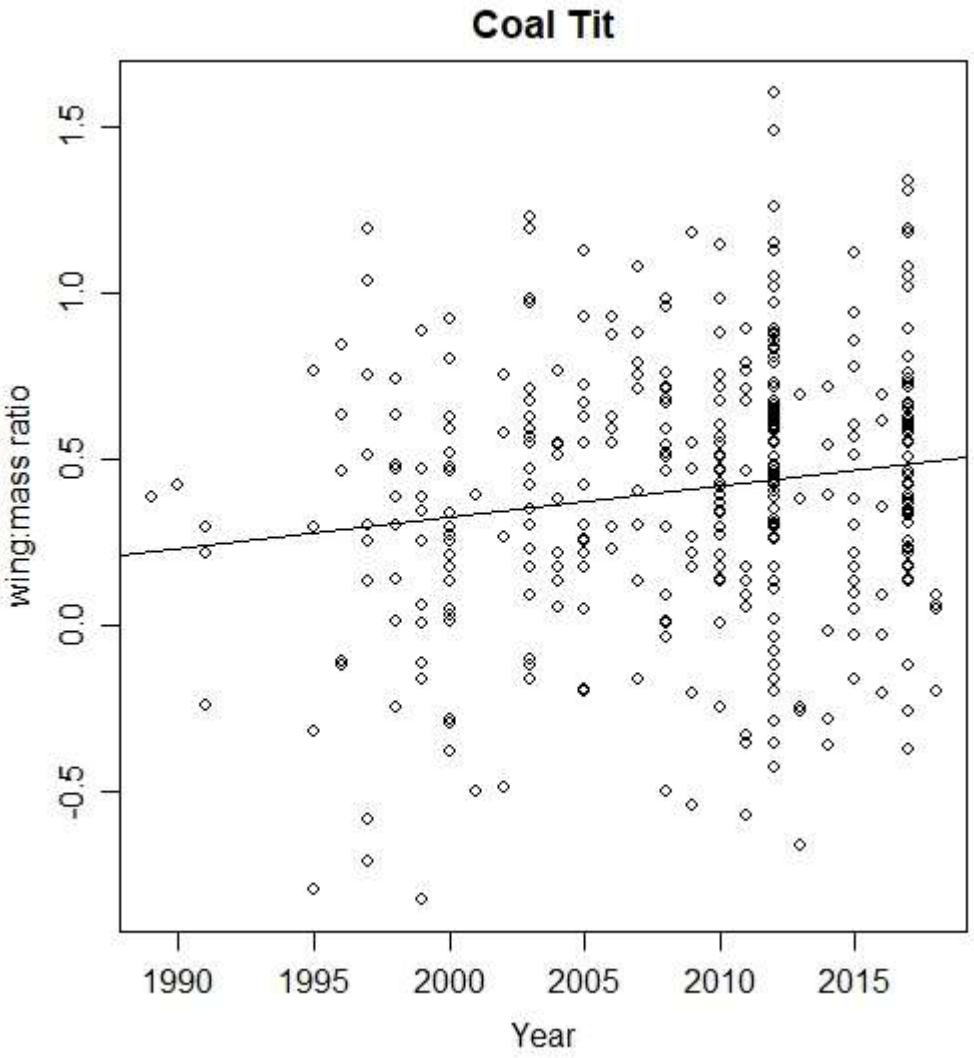

Figure S3. Significant effect of year on the scaled wing:mass ratio in Coal Tits (y = 0.009x - 18.63, df = 385, *P* <0.01) using a linear model (response variable: wing:mass ratio, explaining variable: year) with the function 'lm'.

Table S3. Single-species models for the effect of elevation (continuous (in m x 10^3)) on the bird's scaled (z score) wing length and body mass as well as the wing:mass ratio (ratio), modelled with linear models (function 'lm').

Species	LM	Intercept ± se	Estimate (elevation) ± se	Sample size (No. of individuals)	*P*-value	R^2
Blackbird *Turdus merula*	Wing length ~ elevation	-0.173 ± 0.069	**0.266 ± 0.091**	734	**0.004**	0.010
	Body mass ~ elevation	0.037 ± 0.068	-0.031 ± 0.090	734	0.72	-0.001
	Ratio ~ elevation	-0.518 ± 0.030	**0.120 ± 0.039**	734	**0.002**	0.012
Eurasian Wren *Troglodytes troglodytes*	Wing length ~ elevation	-0.127 ± 0.263	0.152 ± 0.264	49	0.57	-0.014
	Body mass ~ elevation	0.068 ± 0.264	-0.081 ± 0.265	49	0.76	-0.019
	Ratio ~ elevation	-2.840 ± 0.116	0.100 ± 0.117	49	0.42	-0.007
Coal Tit *Periparus ater*	Wing length ~ elevation	0.008 ± 0.225	-0.007 ± 0.144	386	0.96	-0.003
	Body mass ~ elevation	1.380 ± 0.207	**-0.904 ± 0.133**	386	**< 0.001**	0.105
	Ratio ~ elevation	0.044 ± 0.089	**0.238 ± 0.057**	386	**< 0.001**	0.040
Goldcrest *Regulus regulus*	Wing length ~ elevation	-0.895 ± 1.131	0.700 ± 0.904	24	0.48	-0.017
	Body mass ~ elevation	-0.413 ± 0.978	0.421 ± 0.781	24	0.60	-0.030
	Ratio ~ elevation	0.560 ± 0.407	0.188 ± 0.325	24	0.57	-0.029
Black Redstart *Phoenicurus ochruros*	Wing length ~ elevation	-0.120 ± 0.226	0.146 ± 0.241	167	0.55	-0.004
	Body mass ~ elevation	0.053 ± 0.218	-0.026 ± 0.233	167	0.91	-0.006
	Ratio ~ elevation	-1.751 ± 0.099	0.070 ± 0.106	167	0.51	-0.003
Willow Tit *Poecile montanus*	Wing length ~ elevation	-1.228 ± 0.397	**0.857 ± 0.266**	71	**0.002**	0.12

Body mass ~ elevation	-0.933 ± 0.409	**0.651 ± 0.274**	71	**0.02**	0.06
Ratio ~ elevation	-0.516 ± 0.161	0.156 ± 0.107	71	0.15	0.015

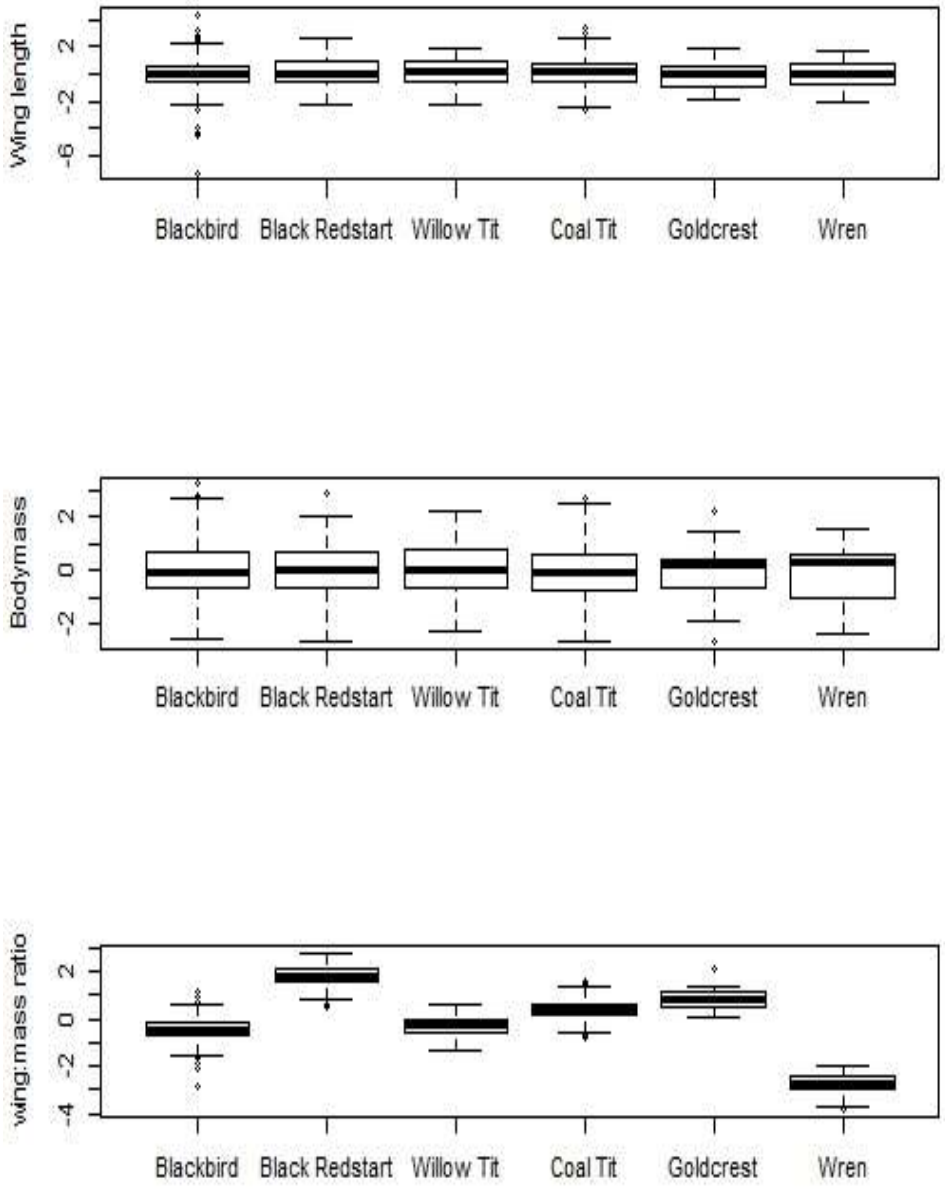

Figure S4. Boxplots show a similar variability in the scaled biometrics across the study species. All available data across all elevations included. Slightly higher variability seems to occur in Blackbirds and Coal Tits. Inter-species variability is highest in the wing:mass ratio.